

# Chapter 12

## Strategies to Alleviate Salinity Stress in Plants



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**Abstract** Soil salinization is a major threat to agriculture in arid and semiarid regions. Besides the identification and use of salt-adapted species or cultivars in saline areas, the use of treatments to alleviate the effects of salinity stress is a promising solution to ensure crop production in such adverse conditions. Chemical, biological, and physical treatments are being successfully applied to seeds, seedlings, or plants before exposure to salinity stress. These treatments activate physiological and molecular pathways enabling the seed or plant to respond more quickly and/or more vigorously after exposure to salinity. Coupled to this, agricultural management practices have also contributed to mitigation of the effects of excessive salt accumulation in the soil. The acquired fundamental knowledge about how a plant reacts to high salt concentrations has been essential for the development of educated and applied strategies for salinity alleviation. In this chapter, we provide a general overview of the main strategies applied to alleviate salinity effects in plants, with a critical discussion of the main achievements described in this field.

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**Keywords** Abiotic stresses · Alleviation strategies · Biological treatments · Chemical treatments · Crops · Field management practices · Halopriming · Ionizing radiation · Magnetic field · Osmopriming · Physical treatments · Plant growth-promoting rhizobacteria · Rhizospheric fungi · Salinity

## Abbreviations

ABA	Abscisic acid
ACC	1-Aminocyclopropane-1-carboxylic acid
AMF	Arbuscular mycorrhizal fungi
APX	Ascorbate peroxidase
BABA	$\beta$ -Aminobutyric acid
CaCl <sub>2</sub>	Calcium chloride
CAT	Catalase
CuSO <sub>4</sub>	Copper sulfate
EC	Electrical conductivity
EMF	Electromagnetic field
ET	Ethylene
FAO	Food and Agriculture Organization
GA <sub>3</sub>	Gibberellic acid
H <sub>2</sub> O <sub>2</sub>	Hydrogen peroxide
H <sub>2</sub> S	Hydrogen sulfide
IAA	Indoleacetic acid
JA	Jasmonate
K <sup>+</sup>	Potassium
K <sub>3</sub> PO <sub>4</sub>	Tripotassium phosphate
KCl	Potassium chloride
KH <sub>2</sub> PO <sub>4</sub>	Monopotassium phosphate
KNO <sub>3</sub>	Potassium nitrate
KOH	Potassium hydroxide
MDA	Malondialdehyde
MF	Magnetic field
MgSO <sub>4</sub>	Magnesium sulfate
Na <sup>+</sup>	Sodium
NaCl	Sodium chloride
NCBI	National Center for Biotechnology Information
NO	Nitric oxide
NO <sub>3</sub>	Nitrate
n-Si	Nanosilicon particles
n-SiO <sub>2</sub>	Nanosilicon dioxide particles
O <sub>2</sub> <sup>-</sup>	Superoxide radical

OH <sup>-</sup>	Hydroxyl radical
P5CR	Pyrroline-5-carboxylate reductase
P5CS	Pyrroline-5-carboxylate synthetase
PEG	Polyethylene glycol
PGPB	Plant growth-promoting bacteria
PGPR	Plant growth-promoting rhizobacteria
POX	Peroxidase
Put	Putrescine
QTL	Quantitative trait locus
RONSS	Reactive oxygen–nitrogen–sulfur species
ROS	Reactive oxygen species
SA	Salicylic acid
SMF	Static magnetic field
SNP	Sodium nitroprusside
SOD	Superoxide dismutase
Spd	Spermidine
Spm	Spermine
UV	Ultraviolet radiation
ZnSO <sub>4</sub>	Zinc sulfate

## 12.1 Introduction

Soil salinization is a major threat to agriculture in arid and semiarid regions, where water scarcity and inadequate drainage of irrigated lands severely reduce crop yield (Hanin et al. 2016). According to information available at the Food and Agriculture Organization (FAO) Soils Portal (<http://www.fao.org/soils-portal/soil-management>), more than 6% of the world's total land area is affected by salt accumulation. The same source indicates that the total area of saline soils has been estimated at 397 million hectares, while sodic soils represent 434 million hectares. This threatening scenario could be exacerbated presently by the emerging climate changes observed in different areas of the world.

Salinization can broadly refer to the accumulation of different salts, including potassium, magnesium, calcium and sodium carbonates, bicarbonates chlorides, and sulfates (Bockheim and Gennadiyev 2000). Consequently, this diverse ionic composition will result in a wide range of physiochemical properties. The literature discussing salt-affected soils often uses two different concepts: soil salinization and soil sodicity. According to the FAO Soils Portal, salt-affected soils can be divided into saline, saline–sodic, and sodic, depending on salt amounts, types of salt, the amount of sodium present, and soil alkalinity. Saline soils are those that have a saturation soil paste extract electrical conductivity (EC) of more than 4 dS m<sup>-1</sup> at 25 °C (which corresponds to approximately 40 mM sodium chloride (NaCl)), generating an osmotic pressure of approximately 0.2 MPa (Grieve et al. 2008;

Munns and Tester 2008). Soil sodicity is a term more restricted to the amount of  $\text{Na}^+$  held in the soil. High sodicity (more than 5% of  $\text{Na}^+$  in the overall cation content) causes clay to swell excessively when wet, therefore severely limiting air and water movements and resulting in poor drainage (Munns 2005; Hanin et al. 2016). Because of the nature of salts present in sodic soils, they are usually alkaline—an aspect also limiting crop cultivation. Saline–sodic soils have, as the name indicates, intermediate properties.

A growing body of research has discussed the effects of soil salinity on plant responses (for recent reviews, see Munns and Gilliham (2015); Hanin et al. (2016); Negrão et al. (2017)). The response of plants to salinity can be described in two main phases, reflecting a time frame of biological processes occurring: shoot ion-independent (early) responses and ion-dependent (late) responses (Negrão et al. 2017). An early response (a couple of minutes or a day after stress imposition) is characterized as a rapid response by the plant, in which the osmotic effect of the salt is sensed in the soil. Early responses are also known as the osmotic phase (Roy et al. 2014). Decreased soil water potential leads to a decline in water uptake by the plant, causing stomatal closure, reducing photosynthesis, and inhibiting leaf expansion, which results in a decrease in the shoot growth rate (Munns and Tester 2008; Das et al. 2015; Nongpiur et al. 2016; Hanin et al. 2016). The ionic phase happens when salts' toxic effects are sensed within the plant because of their accumulation (Munns 2005). The second phase is a slower response occurring after several days to weeks and takes place after toxic accumulation of  $\text{Na}^+$  in photosynthetic tissues (Roy et al. 2014). As a result of the salt accumulation over time, there is a slower inhibition of growth, occurring especially in older leaves, causing their senescence (Munns and Tester 2008). In contrast to young leaves, old leaves are not capable of diluting the salt that enters their cells, and this leads to their death. If the leaves' death rate is higher than the leaves' production rate, then the photosynthetic capacity will be impaired, leading to a reduced growth rate (Munns and Tester 2008; Nongpiur et al. 2016).

According to Negrão et al. (2017), salinity tolerance mechanisms in plants can be classified into three different categories: ion exclusion, which refers to net exclusion of toxic ions from the shoot; tissue tolerance, which refers to compartmentalization of toxic ions in specific tissues, cells, and subcellular organelles; and shoot ion-independent tolerance, which focuses on maintenance of growth and water uptake independent of the extent of  $\text{Na}^+$  accumulation in the shoot. For a detailed description of the main physiological, cellular, and metabolic responses activated in each case, see Munns and Tester (2008); Roy et al. (2014). Nevertheless, it is worth highlighting that ion transport via cell membranes is the basic factor determining salinity tolerance (Ismail and Horie 2017). Moreover, salinity leads to oxidative stress in plants because of production of reactive oxygen species (ROS) such as superoxide radicals ( $\text{O}_2^-$ ), hydrogen peroxide ( $\text{H}_2\text{O}_2$ ), and hydroxyl radicals ( $\text{OH}^-$ ), which can trigger DNA and cellular damage (El-Mashad and Mohamed 2012). To cope with this, antioxidative stress defenses are triggered through enzymatic antioxidant mechanisms including catalase (CAT), superoxide dismutase (SOD), and peroxidase (POX), among others (Gharsallah et al. 2016).

Under salt stress, concomitant accumulation of compatible solutes occurs with the accumulation of solutes in the cytosol (Munns and Tester 2008). Low-weight solutes such as proline, polyols, amino acids, proteins, and betaine—commonly referred to as compatible solutes—play a role in both osmoprotection and osmotic adjustment under high salt concentrations (El-Mashad and Mohamed 2012; Gharsallah et al. 2016). Indeed, overproduction of proline in plants imparts stress tolerance by maintaining cell turgor or osmotic balance; stabilizing membranes, thereby preventing electrolyte leakage; and bringing concentrations of ROS within normal ranges, thus preventing oxidative bursts in plant (Hayat et al. 2012).

Plant morphology, biochemistry, and physiology also play a major role in shaping the different degrees of salinity tolerance (Nongpiur et al. 2016). Among plants there is a gradient of NaCl tolerance in the environment, from the very tolerant ones to the very sensitive ones. Species of the genera *Tecticornia* or *Atriplex* fall into the salt-tolerant group and are often termed halophytes (Munns and Tester 2008; Flowers and Colmer 2015). Rice (*Oryza sativa*) has been described as one of the species most sensitive to salinity (Das et al. 2015). In the field, where the salinity can rise to 100 mM NaCl (about 10 dS m<sup>-1</sup>), rice will die before maturity, while wheat (*Triticum aestivum*) will still be able to produce a reduced yield (Munns et al. 2006). Thus, wheat is considered a moderately salt-tolerant crop. On the other hand, barley (*Hordeum vulgare*) is considered one of the most salt-tolerant cereals, but it dies after extended periods at salt concentrations higher than 250 mM NaCl (equivalent to 50% seawater) (Munns et al. 2006). These examples allow us to conclude that understanding of the mechanism by which crop production could be maintained in a saline growing scenario is needed to ensure our food security (Landi et al. 2017). Differences in salinity responses can occur within the same genus. As an example, in the *Brassica* genus, *B. napus* is the most tolerant species, followed by *B. juncea* and then by *B. oleracea* (Chakraborty et al. 2016).

There have been significant breakthroughs in the understanding of the mechanisms, control, and modulation of Na<sup>+</sup> accumulation in plants (Munns and Tester 2008). Numerous genes have been identified that could be used in molecular breeding programs. As an example, *Saltol*, a major quantitative trait locus (QTL) for salt tolerance, is being transferred into seven popular locally adapted rice varieties: ADT45, CR1009, Gayatri, MTU1010, PR114, Pusa 44, and Sarjoo 52 (Singh et al. 2016). In another study, transgenic tomato plants overexpressing a vacuolar Na<sup>+</sup>/H<sup>+</sup> antiporter were able to grow, flower, and produce fruit in the presence of 200 mM NaCl (Zhang and Blumwald 2001). Despite the success of these approaches, they are time consuming and likely not accessible to all salinity-devoted researchers or farmers, because of their cost. In this context, the development of easy and cost-effective approaches to mitigate the impacts of salinity stress in plants and crop production is highly desirable.

One strategy to mitigate the effects of salt stress in plants could be the application of chemical, biological, and physical treatments in seeds, seedlings, or plants before exposure to salinity stress (see Fig. 12.1). Those treatments, mainly applied before seed sowing, are expected to activate physiological and molecular pathways



**Fig. 12.1** Schematic representation of the multiple strategies available to alleviate salinity stress in plants. *UV* ultraviolet

enabling the seed to respond more quickly and/or more vigorously after exposure to an abiotic stress factor. This chapter aims to provide a general overview of the main treatments applied to plants to alleviate salinity effects, with a critical discussion of the main achievements described in this field.

## 12.2 Chemical Strategies to Alleviate Salinity Stress

Seed and plant priming constitutes a technology to enhance plant tolerance of various abiotic stresses including salinity. Seed priming is generally defined as a pre-sowing treatment, applied before germination, to improve the speed and uniformity of germination (Paparella et al. 2015). The efficiency of the priming technology depends on the plant species, the method of treatment and its duration, and the dose of the protectant/priming agent used (Nawaz et al. 2013; Jisha and Puthur 2016).

Nevertheless, the concept of priming can be further extended to seedlings and whole plants. In this context, plant priming is a mechanism leading to a physiological state that enables plants to respond more rapidly and/or more robustly after exposure to biotic or abiotic stresses (Aranega-Bou et al. 2014). Plant priming can be initiated naturally in response to an environmental stress event, which acts as a cue indicating an increased probability of facing that specific stress factor in the future (Savvides et al. 2016).

Salinity stress can be alleviated by the use of many chemical agents. Some of them are natural metabolites produced by plants in small amounts but, if applied exogenously, they alter gene expression and regulation of metabolism, leading to enhanced salt tolerance. Those substances include sugars (e.g., trehalose), amino acids and their derivatives (e.g., proline, glycine betaine, melatonin,  $\beta$ -aminobutyric acid (BABA), and glutathione), plant growth regulators (e.g., jasmonate (JA) and salicylic acid (SA)), polyamines (e.g., spermine (Spm), spermidine (Spd), and putrescine (Put)), and vitamins, which are involved in the integration of stress signals (Vaishnav et al. 2016). Under salt stress conditions, they could also play a role as osmoprotectants or antioxidants. Another group of chemical agents effective in inducing plant tolerance of abiotic stresses are reactive oxygen–nitrogen–sulfur species (RONSS), which are known also for their damaging activity if they occur in a high concentration. This group of compounds includes reactive molecules containing oxygen (e.g.,  $H_2O_2$ ), sulfur (e.g., hydrogen sulfide ( $H_2S$ )), and nitrogen (e.g., nitric oxide (NO)). Numerous plant stress physiology studies have been devoted to studying the role of sodium nitroprusside (SNP), an inorganic compound that is a source of NO (Vaishnav et al. 2016; Savvides et al. 2016).

Chemical pretreatment of plants before stress occurrence increases their tolerance of adverse environmental conditions, since it contributes to plants responding faster and more strongly to unfavorable conditions (Savvides et al. 2016). A nonexhaustive list of chemical priming treatments targeting the improvement of seed, seedling, and plant salt stress tolerance is presented in Table 12.1. Seed germination is a critical step in plant development. In many crops, germination may be delayed and growth of seedlings inhibited under saline conditions. Consequently, it is not surprising that a large body of research is focused on understanding seed priming, as well as developing new priming protocols. The application of chemical agents for plant and seed pretreatment seems to be an inexpensive method of crop protection from salinity stress because the compounds have been shown to be effective in low concentrations (Savvides et al. 2016). Another benefit is that the tolerance of salinity stress induced by the use of chemical agents becomes systemic although they are usually applied only to the seeds, roots, or leaves. However, most studies have determined plant tolerance of the stress soon after chemical priming. Therefore, the durability of crop protection provided by the aforementioned chemical compounds remains an open question. In Sects. 12.2.1–12.2.4 we discuss some chemical priming approaches described in the literature.

**Table 12.1** Priming treatments adopted for developing salinity stress tolerance in plants

Species	Plant growth stage	Priming agent	Method of application	Reference
Eggplant ( <i>Solanum melongena</i> )	Plant	Proline	Foliar sprayed	Shahbaz et al. (2013)
Rice ( <i>Oryza sativa</i> )	Seedling	Proline, trehalose	Added to medium	Nounjan et al. (2012)
		Silicon	Added to medium	Kim et al. (2014)
		Silicon	Added to soil	Farooq et al. (2015)
	Seed	NaCl, KCl, CaCl <sub>2</sub> , KNO <sub>3</sub> , ascorbic acid, mannitol, PEG, sorbitol, wood vinegar	Soaked in solution	Theerakulpisut et al. (2016)
		Spd, GA <sub>3</sub>	Soaked in solution	Chunthaburee et al. (2014)
Soybean ( <i>Glycine max</i> )	Seed	Proline, glycine betaine	Soaked in solution	Vaishnav et al. (2016)
		KNO <sub>3</sub>	Soaked in solution	Miladinov et al. (2015)
Wheat ( <i>Triticum aestivum</i> )	Seed	Cysteine	Soaked in solution	Nasibi et al. (2016)
		Choline	Soaked in solution	Salama and Mansour (2015)
		CaCl <sub>2</sub>	Soaked in solution	Tamini (2016)
	Seedling	Proline	Foliar sprayed	Talat et al. (2013)
Faba bean ( <i>Vicia faba</i> )	Seed	Melatonin	Soaked in solution	Dawood and El-Awadi (2015)
		Ascorbic acid, nicotinamide	Soaked in solution	Azooz et al. (2013)
		Salicylic acid	Soaked in solution	Anaya et al. (2018)
	Seed/seedling	Silicon	Added to medium/foliar sprayed	Abdul Qados and Moftah (2015)
Mung bean ( <i>Vigna radiata</i> )	Seed	Chitosan	Soaked in solution	Sen and Mandal (2016)
		BABA	Soaked in solution	Jisha and Puthur (2016)
Broccoli ( <i>Brassica oleracea</i> )	Seedling	Methyl jasmonate, urea	Foliar sprayed	del Amor and Cuadra-Crespo (2011)

(continued)



**Table 12.1** (continued)

Species	Plant growth stage	Priming agent	Method of application	Reference
Tomato ( <i>Solanum lycopersicum</i> )	Seedling	Spd	Foliar sprayed	Zhang et al. (2016)
		Silicon	Added to medium	Li et al. (2015)
	Seed	Silicon	Treated with solution	Almutaiori (2016)
		PEG	Soaked in solution	Pradhan et al. (2015)
Kentucky bluegrass ( <i>Poa pratensis</i> )	Seedling	Spd	Foliar sprayed	Puyang et al. (2016)
Lentil ( <i>Lens culinaris</i> )	Seed	Silicon	Soaked in solution	Sabaghnia and Janmohammadi (2015)
Zinnia ( <i>Zinnia elegans</i> )	Seedling	Silicon	Added to medium	Manivannan et al. (2015)
Winter cherry ( <i>Physalis angulata</i> )	Seed	PEG	Soaked in solution	de Souza et al. (2016)
Rape ( <i>Brassica napus</i> )	Seed	PEG	Soaked in solution	Kubala et al. (2015)
Cotton ( <i>Gossypium spp.</i> )	Seed	KNO <sub>3</sub>	Soaked in solution	Nazir et al. (2014)
Pepper ( <i>Capsicum annuum</i> )	Seed	KCl, NaCl, CaCl <sub>2</sub>	Soaked in solution	Aloui et al. (2014)
Maize ( <i>Zea mays</i> )	Seed	NaCl, CaCl <sub>2</sub>	Soaked in solution	Gebreegziabher and Qufa (2017)
Black seed ( <i>Nigella sativa</i> )	Seed	KNO <sub>3</sub> , CaCl <sub>2</sub> , NaCl, ZnSO <sub>4</sub> , CuSO <sub>4</sub>	Soaked in solution	Gholami et al. (2015)
Pea ( <i>Pisum sativum</i> )	Seed	KCl, KOH	Soaked in solution	Naz et al. (2014)
Okra ( <i>Abelmoschus esculentus</i> )	Seed	KCl, mannitol, CaCl <sub>2</sub>	Soaked in solution	Dkhil et al. (2014)
Common bean ( <i>Phaseolus vulgaris</i> )	Seed	Vitamin B <sub>12</sub>	Soaked in solution	Keshavarz and Modares Sanavy (2015)
Tobacco ( <i>Nicotiana rustica</i> )	Plant	Ethanolamine	Added to medium	Rajaeian and Ehsanpour (2015)

BABA  $\beta$ -aminobutyric acid, GA<sub>3</sub> gibberellic acid, PEG polyethylene glycol, Spd spermidine

### 12.2.1 *Amino Acids and Their Derivatives*

Proline is an amino acid acting as an osmoprotectant, which plays an important role in reducing oxidative stress when plants are coping with abiotic stresses (Kavi Kishor and Sreenivasulu 2014; Per et al. 2017). Under stress, plants usually increase the production of endogenous proline. Therefore, exogenous application of this amino acid has been considered a promising way to alleviate salinity effects. Shahbaz et al. (2013) reported that foliar-sprayed proline ameliorated the adverse effect of salinity on the shoot fresh weights of two tested eggplant cultivars and water use efficiency in one of them. Addition of proline to the media in which rice seedlings were grown caused upregulation of proline synthesis genes encoding pyrroline-5-carboxylate synthetase (P5CS) and pyrroline-5-carboxylate reductase (P5CR) and a further increase in endogenous proline (Nounjan et al. 2012). However, exogenous proline also reduced the activity of four antioxidant enzymes (SOD, POX, ascorbate peroxidase (APX), and CAT) and uptake of sodium ions, resulting in a low  $\text{Na}^+/\text{K}^+$  ratio. In the same experiment, trehalose was also tested. This nonreducing sugar was shown to be less effective in limiting  $\text{Na}^+$  uptake and simultaneously decreased production of endogenous proline. Although proline and trehalose did not overcome growth limitation under salt stress, they showed a beneficial impact during the stress recovery period (Nounjan et al. 2012).

Pretreatment of wheat (*T. aestivum*) seeds with cysteine enhanced tolerance of salinity stress, increasing the activity of antioxidant enzymes and decreasing ion toxicity (Nasibi et al. 2016). The beneficial effect of cysteine on wheat plants can be attributed to production of either glutathione or  $\text{H}_2\text{S}$ —molecules that are well known for their antioxidant roles. Mung bean (*Vigna radiata*) seeds treated with BABA showed positive effects against salt stress via accumulation of proline, total protein, and carbohydrate in seedlings (Jisha and Puthur 2016). Moreover, the activities of antioxidant enzymes increased in BABA-primed seeds. The biomass of seedlings raised from primed seeds was increased in comparison with nonprimed ones, under stressed and unstressed conditions. On the basis of these findings, the authors concluded that seed priming with BABA is a cost-effective technique and a promising strategy to overcome negative effects of salinity stress and, likely, other abiotic stresses in crops.

Dawood and El-Awadi (2015) studied the suitability of using melatonin as a priming agent. In this work, seeds of faba bean (*Vicia faba*) were soaked in a melatonin solution and the seedlings were irrigated with diluted seawater. Interestingly, the application of melatonin showed beneficial features, since it improved growth parameters, relative water content and the contents of photosynthetic pigments, total carbohydrates, total phenolics, and indoleacetic acid (IAA). Melatonin treatment also reduced the contents sodium and chloride ions.

### 12.2.2 Polyamines and Vitamins

The effect of salt stress can be alleviated in crops through prior treatment with compounds belonging to the polyamine family (Zhang et al. 2016). Spd, Spm, and Put are polyamines that are naturally present in plant tissues. Their content usually increases under salinity stress because they are able to alleviate its effects. They can interact with membrane phospholipids, thus stabilizing cellular structures. Polyamines also stabilize the structures of many enzymes and maintain  $K^+/Na^+$  homeostasis by limiting  $Na^+$  uptake by roots and limiting loss of  $K^+$  by shoots (Zhao et al. 2007). Furthermore, polyamines neutralize ROS induced under salt stress and thus protect cells from oxidative damage (Puyang et al. 2016). Exogenous Spd was used for foliar spraying of young tomato plants, which were then exposed to salinity–alkalinity stress 7 days later (Zhang et al. 2016). The results showed that Spd caused a decrease in ROS and malondialdehyde (MDA) content. Also, a simultaneous increase in antioxidant enzyme activities and nonenzymatic components of the antioxidant system was noticed, which resulted in chloroplast protection from damage because of the stress. Likewise, an improvement in the salinity tolerance of Kentucky bluegrass by exogenous Spd treatment was reported by Puyang et al. (2016). The grass leaves were sprayed with Spd twice before being exposed to NaCl solution for 28 days. Spd treatment mitigated decreases in the  $K^+/Na^+$  ratio and in the content of chlorophyll, potassium, calcium, and magnesium ions. Moreover, the treatment also resulted in a reduction in electrolyte leakage and  $Na^+$  content and caused an increase in the content of endogenous osmoprotectants such as proline, Spm, and Spd. Khan et al. (2012) reported that seed priming with polyamines (Spd, Spm, and Put) enhanced the germination and early growth of hot pepper seedlings (*Capsicum annuum*) in comparison with untreated seeds.

Other interesting findings were described by Chunthaburee et al. (2014), who treated rice seeds with Spd and gibberellic acid ( $GA_3$ ). This combined treatment enhanced the antioxidant system in the plants and reduced the production of  $H_2O_2$ . Moreover, Spd and  $GA_3$  priming improved ion homeostasis and delayed the loss of pigments. Although the application of these substances improved the growth of seedlings, the beneficial effect was quantitatively small, which might limit their use in a seed technology context.

Seed priming with vitamins has been revealed to be an approach that could stimulate the growth of legume and cereal seedlings under unfavorable conditions. Faba bean seeds treated with ascorbic acid and nicotinamide showed increased content of photosynthetic pigments, soluble carbohydrates and proteins, proline, and other amino acids, whereas transpiration and ion leakage decreased (Azooz et al. 2013). The application of nicotinamide was found to be more effective in the alleviation of salt stress effects than ascorbic acid. However, the combination of these two vitamins resulted in an enhanced synergistic effect. Priming seeds of common bean (*Phaseolus vulgaris*) with vitamin  $B_{12}$  also increased the survival capacity of bean

plants. This positive effect was due to concomitant stimulation of antioxidant enzyme activity and reduction of ROS (Keshavarz and Modares Sanavy 2015). Application of choline enhanced salt tolerance in wheat through stimulation of membrane biosynthesis to maintain plasma membrane stability, fluidity, and therefore ion homeostasis (Salama and Mansour 2015).

### **12.2.3 Plant Growth Regulators and Organic or Inorganic Compounds**

Another essential group of chemical agents that play a major role in adaptation to stresses, including salinity, are plant growth regulators. They affect plant growth and development, and induce defense against a variety of abiotic stresses. Application of SA on faba bean seeds resulted in a positive effect on germination parameters and improved establishment of seedlings (Anaya et al. 2018). This work also highlighted that this beneficial response is dose dependent, with the lowest applied concentration of SA being the one with the most positive effect, even under strong salinity.

Salinity stress may also be alleviated by application of nitrogen fertilizer such as urea, which is commonly used in agriculture. Foliar application of this compound on broccoli plants grown at 40 mM NaCl allowed maintenance of growth, gas exchange, and leaf N-NO<sub>3</sub> concentrations at levels similar to those in nonsalinized plants (del Amor and Cuadra-Crespo 2011). Similar results were obtained when methyl jasmonate was used in the same way. Foliar application of both urea and methyl jasmonate became ineffective when a threefold increase in salinity was applied.

In soybean, priming of seeds with NO, applied as SNP, played a protective role in germination and seedling development under salinity stress (Vaishnav et al. 2016). The germination rate of SNP-primed seeds under salinity conditions was 82% higher than that of untreated seeds. Interestingly, SNP treatment seemed to have an impact on plant architecture, resulting in longer seedlings with more lateral roots. Treated seedlings also accumulated more chlorophyll and showed a higher content of endogenous proline than untreated seedlings or those treated with other tested substances (glycine betaine, mannitol, or proline). They also exhibited a reduced MDA content, which indicated lower lipid peroxidation. The overall results indicated that a myriad of plant protective responses are activated in response to SNP priming, which may be of relevance to development of new seed treatments.

Much attention has been devoted to investigating the usefulness of silicon (Si) in the alleviation of salinity stress in crops. It is a very common element in nature, and its role in plant stress tolerance is complex and multifaceted (Yin et al. 2016). First of all, it is a component of the double-layer cuticle, being the first physical barrier limiting transpiration during salinity stress. Other roles of silicon in response to salinity have been postulated, including maintenance/improvement of water status and a decrease in oxidative damage (Yin et al. 2016). Last, but not least, silicon reduces concentrations of Na<sup>+</sup> ions and limits their transportation, resulting in alleviation of salinity (Manivannan et al. 2015; Kim et al. 2014). Priming treatments

with nanosilicon (n-Si) and nanosilicon dioxide (n-SiO<sub>2</sub>) particles resulted in improved germination of lentil (*Lens culinaris*) (Sabaghnia and Janmohammadi 2015) and tomato seeds (Almutaori 2016) under salt stress. Seedling traits such as weight, root length, and shoot length were also positively affected. The authors concluded that application of nanomaterials on seeds may stimulate defense mechanisms of plants and increase salinity tolerance in other crops. The role of silicon and nanosilicon in the mitigation of salt stress in faba beans was investigated by Abdul Qados and Moftah (2015). Both forms of silicon were effective in improving the salt tolerance of plants by increasing plant height, fresh and dry weight, and total yield under salt conditions. In a hydroponic system, silicon supplementation of *Zinnia elegans* resulted in alleviation of salinity stress induced by NaCl treatment (Manivannan et al. 2015). Silicon-treated plants displayed enhanced growth and improved photosynthetic parameters. Moreover, silicon improved membrane integrity, resulting in reduced electrolyte leakage potential and lipid peroxidation levels (Manivannan et al. 2015). Silicon was also shown to increase the activity of antioxidant enzymes in rice, which contributed to reduced levels of oxidative damage (Kim et al. 2014). In tomato, exogenous silicon application affected seedling tolerance of salinity stress (Li et al. 2015). Silicon treatment improved tomato growth, photosynthetic pigment and soluble protein content, the net photosynthetic rate, and root morphological traits under salt stress. One interesting aspect of this study was the fact that the leaf transpiration rate and stomatal conductance were not decreased but increased by application of silicon under salt stress (Li et al. 2015). Silicon has been described as modulating the level of stress-related plant growth regulators such as JA, SA, and abscisic acid (ABA). Kim et al. (2014) monitored the content of these molecules in rice roots under salinity stress after application of silicon and noted that the levels of ABA were higher 6 and 12 hours after treatment but became insignificant after 24 hours. The authors concluded that the uptake of greater silicon amounts limits the activation of ABA metabolism, which regulates stomatal conductance during stress conditions, contributing to the improved performance of silicon-treated plants under salinity.

Some natural polysaccharides have shown beneficial effects in plant protection against salt stress. As an example, Sen and Mandal (2016) tested the response of mung bean seeds primed with chitosan under NaCl stress. Chitosan promoted seed germination and seedling growth, particularly in the early phase of growth.

#### ***12.2.4 Exploring the Potentialities of Osmopriming and Halopriming***

Osmopriming has unexploited potential to improve crop response to salinity. This seed-priming method involves treatment of seeds with solutions with a low water potential (e.g., an osmotic solution). Numerous chemicals are used in the seed osmopriming technique, including polyethylene glycol (PEG), mannitol, and

sorbitol (Nawaz et al. 2013; Paparella et al. 2015). Soaking of seeds in such a low-water-potential solution enables a slow imbibition that is sufficient to trigger seed germination metabolic processes; however, germination remains inhibited. The impacts of osmopriming on the activation of many enzymes, DNA damage, and repair responses, as well as on the modulation of ROS-mediated damage of cellular components, has been reviewed extensively (for an example, see Paparella et al. 2015).

Primed seeds usually germinate faster and more uniformly (Nawaz et al. 2013). The most commonly used osmotic agent in osmopriming is PEG, which is often used in combination with ionic salts. Osmoprimed seeds have showed improved vigor and germination under salt stress. As an example, Pradhan et al. (2015) primed tomato (*Solanum lycopersicum*) seeds with PEG 6000 and observed resulting beneficial effects on the germination percentage, vigor index, and seedling dry weight under salt stress. Kubala et al. (2015) also used PEG 6000 to prime seeds of *B. napus* and noted that PEG treatment improved germination and seedling growth under salinity stress. Additionally, these authors demonstrated that this improved phenotype was connected with a significant increase in proline content. PEG 8000 was used as a seed-priming agent in *Physalis angulata* under saline conditions (de Souza et al. 2016). The authors observed that this treatment resulted in higher germination percentages and uniformity under saline conditions. Moreover, seedlings showed relatively normal growth and had slightly greater biomass. The authors concluded that priming induced the activation of physiological mechanisms responsible for osmotic adjustment and synthesis of proteins involved in defense against free radicals. The authors also suggested that such responses reflect reprogramming of the transcriptome under such conditions, resulting in upregulation of genes related to ion transport and genes encoding antioxidant enzymes (de Souza et al. 2016).

Another promising priming technique is halopriming, which involves soaking seeds in solutions of inorganic salts such as NaCl, potassium chloride (KCl), potassium nitrate (KNO<sub>3</sub>), tripotassium phosphate (K<sub>3</sub>PO<sub>4</sub>), monopotassium phosphate (KH<sub>2</sub>PO<sub>4</sub>), magnesium sulfate (MgSO<sub>4</sub>), or calcium chloride (CaCl<sub>2</sub>) (Nawaz et al. 2013). Priming seeds of cotton and soybean with KNO<sub>3</sub> had a positive effect on germination and seed vigor under salinity stress (Miladinov et al. 2015; Nazir et al. 2014). Similarly, seed priming with different salts—KCl, NaCl, and CaCl<sub>2</sub>—showed a positive effect on germination in pepper under salt stress by speeding up imbibition, which enabled faster metabolic activity in the seeds (Aloui et al. 2014). In maize (*Zea mays*), seed priming with NaCl and CaCl<sub>2</sub> increased germination and seedling growth parameters in comparison with nonprimed seeds under salt stress (Gebreegziabher and Qufa 2017). Interestingly, those two priming treatments showed different impacts on maize physiology. While NaCl priming improved crop maturity and yield, CaCl<sub>2</sub> priming accelerated the germination process.

The efficiency of salt priming for seedling growth has been extensively examined in the literature. Priming agents such as KNO<sub>3</sub>, CaCl<sub>2</sub>, NaCl, zinc sulfate (ZnSO<sub>4</sub>), and copper sulfate (CuSO<sub>4</sub>) were tested to overcome salinity effects in black seed (*Nigella sativa*) (Gholami et al. 2015). Among the tested compounds, NaCl was the

most effective in the alleviation of an adverse effect of salt stress, promoting efficient germination. Despite the primacy of NaCl, KNO<sub>3</sub>, CaCl<sub>2</sub>, and ZnSO<sub>4</sub> were also effective in promoting germination performance and seedling development but to a lesser extent (Gholami et al. 2015). *Pisum sativum* seeds primed with KCl and potassium hydroxide (KOH) showed improvements in the germination percentage and seedling growth (Naz et al. 2014). When wheat seeds were primed with CaCl<sub>2</sub>, salinity tolerance of the seedlings was improved, as seen by their enhanced growth (Tamini 2016). A deeper investigation of mechanisms triggered by priming showed that cell membranes were stabilized, chlorophyll content and activity of nitrate reductase were enhanced, and accumulation of proline, total soluble sugars, and proteins occurred. On the basis of this, the author suggested that priming of seeds with CaCl<sub>2</sub> successfully triggers physiological and metabolic processes that could support wheat cultivation in salt-affected soils. In okra (*Abelmoschus esculentus*), seed priming with KCl, CaCl<sub>2</sub>, and mannitol improved the germination percentage, seedling dry weight, and final emergence percentage (Dkhil et al. 2014). Theerakulpisut et al. (2016) compared the effectiveness of ten priming agents—NaCl, KCl, CaCl<sub>2</sub>, KNO<sub>3</sub>, ascorbic acid, mannitol, PEG 6000, sorbitol, wood vinegar (made from eucalyptus), and distilled water—in protection of rice seedlings against salinity stress. Of all tested agents, KNO<sub>3</sub>, mannitol, and wood vinegar were most effective in enhancing growth parameters of seedlings. The application of these compounds allowed maintenance of ion homeostasis while preventing chlorophyll degradation and membrane damage in plant tissues (Theerakulpisut et al. 2016).

Besides seeds, salt treatments have been also successfully applied in plant priming. As an example, Yan et al. (2015) pretreated sweet sorghum plants with NaCl for 10 days, then the plants were stressed with twice as high a concentration of that compound for an additional 7 days. The authors found a higher photosynthetic rate during stress and a smaller reduction of dry matter in pretreated plants than in non-pretreated ones. According to these authors, pretreatment of the plants with the lower salt concentration enhanced their osmotic resistance and reduced root uptake of sodium ions, which highlighted a concerted mechanism to deal with the constraint (Yan et al. 2015).

### 12.3 Biological Treatments to Improve Crop Salinity Tolerance

The identification of physiological responses, as well as biochemical networks involved in halophyte responses to salinity, has provided new salt stress-related genes available for plant improvement. This finding has supported the development of new approaches to alleviate salinity in plants and possibly stimulate crop cultivation in soils with enhanced salt accumulation (Shrivastava and Kumar 2015). Some of these genes have been used in molecular breeding approaches, as genetic engineering, but the effects of introduced genes need to be evaluated in the field to

determine their effects on salinity tolerance and yield improvement (for a review, see Roy et al. 2014). Unfortunately, the ecological interaction of microorganisms inhabiting the roots (the rhizosphere) and leaves (the phyllosphere) of halophytes has been neglected in these studies, but it is important to keep in mind that they may contribute significantly to the halophytes' well-being and salinity tolerance (Ruppel et al. 2013).

Plants are capable of recruiting and forming mutualistic associations with a number of soil microorganisms, with beneficial effects on the plants' productivity and resilience in harsh conditions (De-La-Peña and Loyola-Vargas 2014; Munns and Gilliham 2015; Kasim et al. 2016). The contribution of a specialized microbiome in assisting plants to withstand salinity is often overlooked; however, it can be used as an alternative to the development of salt-tolerant crops through genetic modification (Yuan et al. 2016). Mounting evidence highlights the fact that rhizospheric fungi and plant growth-promoting rhizobacteria (PGPR) found in association with plants help them to acquire some degree of salinity stress tolerance (Campanelli et al. 2012; Habib et al. 2016; Kang et al. 2014; Bal et al. 2013; Gururani et al. 2013; Hajiboland 2013).

### 12.3.1 *Rhizospheric Fungi*

Campanelli et al. (2012) investigated how alfalfa (*Medicago sativa*) plants inoculated with *Glomus viscosum* dealt with NaCl stress. Inoculated alfalfa plants showed diminished progression of tissue wilting and increased plant height, root density, and leaf area in comparison with noninoculated plants. Additionally, mycorrhizal dependency increased at higher NaCl concentrations but, on the other hand, mycorrhizal colonization was negatively affected (Campanelli et al. 2012). Such findings highlight the need to carefully choose microbial species to be used in specific crops. Also, the source of the inoculum—either derived from a culture collection or isolated from a naturally saline environment—must be considered when assessing the potential of these microorganisms to assist plant growth under stressful conditions (Estrada et al. 2013). Isolation of microbial inoculants from plants' natural habitat has been shown to be more efficient in assisting plant acclimation to harsh environments (Bal et al. 2013; Querejeta et al. 2006; Liu et al. 2016). Estrada et al. (2013) concluded that use of native arbuscular mycorrhizal fungi (AMF) from a saline environment was more effective than use of AMF from a culture collection, providing greater protection against oxidative damage and more efficient photosynthetic apparatus and stomatal conductance. Bearing that in mind, some studies have demonstrated that native microbial inoculants isolated from saline soils can perform better and display a greater capacity to promote plant growth (Bharti et al. 2013; Campagnac and Khasa 2013; Damodaran et al. 2014; Liu et al. 2016; Azad and Kaminskyj 2016).



### 12.3.2 Plant Growth–Promoting Bacteria

Plant growth–promoting bacteria (PGPB) or rhizobacteria (PGPR) have been studied for their potential to promote plant growth, serving as an important tool to increase worldwide crop productivity even under salinity. For example, the interaction of *Burkholderia cepacia* SE4 and *Promicromonospora* sp. SE188 with *Cucumis sativus* seedlings (Kang et al. 2014) has been studied. Other studies have included assessment of the effects of *Bacillus pumilus* strain DH-11 in *Solanum tuberosum* plants (Gururani et al. 2013) and *Exiguobacterium oxidotolerans* in *Bacopa monnieri* (Bharti et al. 2013). Common findings in all of these studies were that the microorganism–plant interactions enhanced shoot and root growth, nutrient uptake, chlorophyll content, photosynthetic efficiency, and the  $K^+/Na^+$  ratio in saline environments.

Plant growth regulators have a crucial role in controlling a number of physiological and metabolic processes during plant development and interaction with environmental conditions. Ethylene (ET) is thought to be a coordinator between plant development and their response to stress conditions, including high salt levels (Ma et al. 2012; Ellouzi et al. 2014; Peng et al. 2014; Tao et al. 2015). Concentrations of ET and its precursor 1-aminocyclopropane-1-carboxylic acid (ACC) can increase in plants exposed to such stressful conditions (Habib et al. 2016). Whether the accumulation of ET or ACC has a beneficial or detrimental effect on plant responses to salinity still remains unclear (Tao et al. 2015; Habib et al. 2016). Some studies have pointed out that ET may play a negative role in regulating plant adaptation to salinity, with potential inhibitory effects on root and shoot length and overall plant growth (Barnawal et al. 2014; Nadeem et al. 2014). One way to prevent an inhibitory effect of ET is through accumulation of compounds, such as ACC deaminase, that can interfere with its synthesis, reducing the excess of ET in plants. ACC deaminase–containing PGPR can be used as a way to reduce the deleterious effects that ET accumulation may exert in plants tissues (Bal et al. 2013; Ali et al. 2014; Barnawal et al. 2014; Tao et al. 2015; Habib et al. 2016). Inoculation of rice seed with ACC-utilizing bacteria (*Alcaligenes* spp.) improved plant performance under NaCl-imposed stress (Bal et al. 2013). Association with two bacterial strains containing ACC deaminase—*Bacillus megaterium* UPKR2 and *Enterobacter* sp. UPMR18—led to higher germination rates and biomass accumulation in okra seedlings under NaCl stress, with improved chlorophyll content and ROS-scavenging enzyme activity (Habib et al. 2016). Similar results were obtained with *P. sativum* inoculated with the ACC deaminase–containing rhizobacterium *Arthrobacter protophormiae* SA3, in which a 60% decrease in ACC content was noted (Barnawal et al. 2014). Besides overcoming the toxic effects of ET-induced damage, inoculation with this rhizobacterium also proved beneficial for nodulation and mycorrhization (Barnawal et al. 2014). The use of other PGPB endophytes from the genus *Pseudomonas* has also been a successful approach to alleviate the toxic effects of salinity stress. Ali et al. (2014) used the ACC deaminase–containing PGPB endophytes *P. fluorescens* YsS6, *P. migulae* 8R6, and ACC deaminase–deficient mutants of them to promote

tomato plant growth in the absence or presence of salt stress. The results showed that tomato plants inoculated with *P. fluorescens* YsS6 and *P. migulae* 8R6 were healthier and accumulated more biomass than noninoculated control plants (Ali et al. 2014). Interestingly, when treated with the corresponding bacterial ACC deaminase–knockout mutants, plants were shown to be more salt sensitive, with a performance similar to that of noninoculated plants, which may lead one to conclude that this enzyme has a direct effect on plant adaptation in response to salt stress (Ali et al. 2014).

As a result of successful plant–microbe interactions, PGPR can further multiply into microcolonies or biofilms, providing additional protection against environmental stresses. In a study carried out by Kasim et al. (2016), *Bacillus amyloliquefaciens* showed the highest biofilm formation while efficiently enhancing growth and recovery of salt-sensitive barley cultivar Giza 123 seedlings under NaCl stress. Similar results were obtained by Chen et al. (2016), who found that *B. amyloliquefaciens* SQR9 conferred salt tolerance in maize plants, improving chlorophyll content and accumulation of total soluble sugar, while alleviating oxidative damage with increasing POX/CAT activity.

## 12.4 Physical Treatments to Alleviate Salinity Stress in Crops

The use of physical methods to increase plant production offers eco-friendly advantages and the possibility of use on a high-throughput scale. Physical invigoration methods (also known as “physical priming”) are an alternative approach to current chemically or biologically based ones. The use of physical invigoration methods has been established as a promising approach to develop new biotech-based solutions for the growing seed market (Araújo et al. 2016). Several reports have described successful use of agents such as temperature; magnetic fields (MFs); or microwave, ultraviolet (UV), or ionizing radiation as promising presowing seed treatments (for reviews, see Paparella et al. 2015; Araújo et al. 2016). In general, presowing exposure to nonlethal doses of these physical agents has a positive impact not only in stimulating germination but also in improving the final quality and physiological performance of the plants, in terms of growth and yield. Presowing temperature treatments are a frequent approach to break seed dormancy, enhancing the overall quality of seed lots (Liu and El-Kassaby 2015). However, in this section we will not focus on thermopriming, because usually it is combined with other priming approaches (hydropriming or osmopriming; see Paparella et al. 2015). To the best of our knowledge, there have been only a few reports describing the use of physical invigoration methods to stimulate salinity tolerance. Nevertheless, we have collected some examples from literature databases, and we discuss their potential application as treatments to alleviate salinity stress in plants.

### 12.4.1 Ionizing Radiation

Gamma rays are known to have several potential applications in agriculture, including crop improvement, depending on the dose of exposure (Ahuja et al. 2014). The characterization of the effects of the gamma rays on seeds is a topic receiving growing attention. Several studies have demonstrated the suitability of low-/high-dose gamma radiation as an efficient seed invigoration treatment (Araújo et al. 2016). Moreover, some recent reports have supported its use as an effective treatment to alleviate salinity effects in plants.

Rejili et al. (2008) examined the effects of the interaction of salinity and gamma radiation on the growth and  $K^+/Na^+$  ionic balance of Gannouch and Mareth populations of *M. sativa* cultivar Gabès. This work analyzed the morphological changes and physiological responses of the two alfalfa populations irradiated with a 350 Gy dose and cultivated in the presence of different salt concentrations for 50 days. The results showed that exposure to gamma radiation, alone or in combination with salt stress, significantly increased shoot numbers, stem height and chlorophyll *b* content in the Gannouch population, while no change occurred in the Mareth population. The authors concluded that the growth of gamma-irradiated plants was stimulated and that these plants were more tolerant of salt stress (Rejili et al. 2008). In a similar approach, Kumar et al. (2017) investigated the effects of presowing gamma radiation seed treatments on pigeon pea (*Cajanus cajan*) plant growth, seed yield, and seed quality under salt stress (80 and 100 mM NaCl) and control (0 mM NaCl) conditions. The study was conducted in two genetically diverse varieties, Pusa-991 and Pusa-992. A positive effect of presowing exposure of seed to low-dose gamma radiation (<0.01 kGy) under salt stress was evident in pigeon pea. Pigeon pea variety Pusa-992 showed a better salt tolerance response than Pusa-991 and, importantly, irradiated plants performed better than nonirradiated plants even at increasing salinity levels. Gamma radiation caused a favorable alteration in the source–sink (shoot–root) partitioning of recently fixed carbon ( $^{14}C$ ), enhanced glycine betaine content, reduced protease activity, reduced the partitioning of  $Na^+$ , and promoted accumulation of  $K^+$  under salt stress. Changes in these traits were important to differentiate between salt-tolerant and salt-susceptible varieties of pigeon pea and impacted on the seed yield and quality under salinity (Kumar et al. 2017). Importantly, these works revealed that the metabolic pathways activated in response to irradiation under salt stress are also genotype dependent.

In another study, Ahmed et al. (2011) investigated the effects of gamma radiation doses (0, 20, 40, and 80 Gy) on damsisia (*Ambrosia maritima*) plants under salt stress. In this work, salt stress was imposed in sandy loam soil (sand-to-loam ratio 3:2) with a mixture of salts ( $NaCl$ ,  $CaCl_2$ , and  $MgSO_4$  in a 2:2:1 ratio). The authors observed that irradiation of damsisia seeds with 40 or 80 Gy increased plant tolerance of salinity, in comparison with control, with regard to plant height, fresh/dry weights, and photosynthetic pigment. Importantly, they reported that irradiation alleviated the adverse effects of salinity by increasing total sugar and total soluble phenols in damsisia plant shoots. These findings provide new clues about metabolic

pathways triggered by irradiation and might contribute to improving the salinity response of these plants.

### ***12.4.2 Magneto-Priming***

The study of the effects of MFs on biological organisms, including plants, dates back to the second half of the nineteenth century (Pietruszewski and Martínez 2015). Several recent reviews have summarized the impacts of MFs on many biological processes in plants, such as growth, development, and metabolism (Maffei 2014; Wolff et al. 2014). Static magnetic fields (SMFs) and electromagnetic fields (EMFs) are used in agriculture for seed priming, also known as “magneto-priming,” with proven beneficial effects on seed germination, vigor, and crop yield (Baby et al. 2011). Recently, some researchers have investigated the suitability of using MFs to alleviate the impacts of salinity in crops and postulated some molecular mechanisms behind this improved response.

Rathod and Anand (2016) reported that magneto-priming (50 mT for 2 h) caused a significant increase in the height, leaf area, and dry weight of wheat plants under nonsaline and saline conditions. In this work, the authors described a decrease in the  $\text{Na}^+/\text{K}^+$  ratio in plants from primed seeds compared with those from unprimed seeds under salinity. Interestingly, magneto-priming seemed to be more beneficial to the salt-sensitive variety (HD 2967) that was studied than to the salt-tolerant one (Kharchia) under saline conditions. The authors concluded that magneto-priming induced tolerance, allowing primed plants to yield similarly under saline conditions as unprimed plants did under normally sown conditions.

The effects of MFs in seed germination and growth of sweet corn under NaCl stress (0, 50, and 100 mM) were investigated (Karimi et al. 2017). Seeds were exposed to weak (15 mT) or strong (150 mT) MFs for 6, 12, and 24 hours. While salinity reduced germination and seedling growth in nontreated seeds, MF-treated seeds showed better performance in terms of the aforementioned traits, regardless of the NaCl concentration tested. The authors also found that the improved response of MF-treated seeds was related to the maintenance of the water content and suggested that MF treatment primed the plant for salinity by  $\text{H}_2\text{O}_2$  signaling. Magnetic field priming for 6 hours was suggested for enhancing germination and growth of sweet corn under salt stress (Karimi et al. 2017). In another study, Kataria et al. (2017) investigated the effects of presowing seed treatment with MFs (200 mT for 1 h) in alleviating the adverse effects of salt stress on germination in soybean and maize. In both species, magneto-primed seeds had enhanced percentage germination and early seedling growth parameter values (root and shoot length, and vigor indexes) under different salinity levels (0–100 mM NaCl) in comparison with untreated seeds. Interestingly, these authors also noticed that the levels of  $\text{O}_2^-$  and

H<sub>2</sub>O<sub>2</sub> in germinating magneto-primed seeds of maize and soybean were also increased. They suggested that increased water uptake, greater activity of hydrolytic enzymes ( $\alpha$ -amylase and protease), and increased free radical content in MF-treated seeds as compared with untreated seeds under both nonsaline and saline conditions enhanced the rate of germination and seedling vigor (Kataria et al. 2017).

### 12.4.3 Ultraviolet Radiation

UV radiation is a part of the nonionizing region of the electromagnetic spectrum and constitutes approximately 8–9% of total solar radiation (Coohill 1989). As a consequence of the stratospheric ozone layer being depleted, the amounts of solar UV radiation reaching the earth's surface are increasing, as is interest in understanding the mechanisms by which plants may protect themselves from this threat (Hollósy 2002). UV exposure triggers specific protective responses in plants, whose molecular signature could be used to design new treatments to improve the response to abiotic constraints as salinity.

The information available regarding the potential use of UV radiation as a salinity alleviation treatment is very limited. To the best of our knowledge, only the work of Ouhibi et al. (2014) is available in the PubMed bibliographic repository of the National Center for Biotechnology Information (NCBI; <https://www.ncbi.nlm.nih.gov>, accessed on the 10<sup>th</sup> August 2017). In this work, lettuce (*Lactuca sativa*) seeds were treated with UV-C radiation in an attempt to improve the resulting seedlings' tolerance of salt stress (Ouhibi et al. 2014). Two levels of UV-C radiation (0.85 or 3.42 kJ m<sup>-2</sup>) were tested, and UV-primed seeds and nonprimed seeds were grown under either nonsaline conditions or 100 mM NaCl. In nonprimed seeds, salt stress resulted in a smaller increase in the fresh weights of roots and leaves, accompanied by a restriction in tissue hydration and K<sup>+</sup> ion uptake, as well as an increase in Na<sup>+</sup> ion concentrations in all organs. These effects were mitigated in plants grown from the UV-C primed seeds, with the salt-mitigating effect of UV-C being more pronounced at 0.85 kJ m<sup>-2</sup> than at 3.42 kJ m<sup>-2</sup>, which suggested a dose-dependent effect of the treatment. The authors suggested that UV-C priming could be used as a simple and cost-effective strategy to alleviate NaCl-induced stress in lettuce (Ouhibi et al. 2014).

UV-C light has been described as a powerful tool for stimulating the synthesis and accumulation of health-promoting phytochemicals (before and after harvest), extending the shelf life of fresh plant products or stimulating plant defenses against biotic attacks (Urban et al. 2016). Consequently, the ability of UV-C to stimulate plant adaptation to abiotic constraints is postulated, and it needs to be further investigated.

## 12.5 Field and Water Management Practices

We have previously described some chemical, physical, and biological treatments that can be exogenously applied to plants. Nevertheless, added value may be obtained if these treatments are coupled to adequate field and water management practices, constituting a useful approach to improvement of soil quality (Li et al. 2016). Such efforts should aim to minimize unproductive water losses, maintain soil salinity at tolerable levels, and enhance organic matter and nutrient availability (Bezborodov et al. 2010). Several technologies have been developed and used to control the aforementioned constraints, including mulching of the soil surface with plastic or crop residues (Pang et al. 2010; Maomao et al. 2014; Zhao et al. 2014; Li et al. 2016), a buried straw layer (Zhao et al. 2014), repellent salinity agents (Shahein et al. 2015), or conservation agricultural practices (Devkota et al. 2015). Mulching of the soil surface, using materials such as crop residues or plastic, is considered to be one of the main options to mitigate the toxic effects of soil salinization, promoting soil quality and consequently increasing crop yield (Bezborodov et al. 2010; Zhang et al. 2014; Xie et al. 2017). As residues are placed on the soil surface, they will shade the topsoil and prevent water loss by evaporation, increase soil moisture accumulation, and help reduce salt accumulation (Li et al. 2013; Li et al. 2016). When the material used derives from crop residues, it additionally assists in building soil organic carbon (Bezborodov et al. 2010; Maomao et al. 2014). As these substrates of natural origin decompose, organic carbon is released into the saline soil and mitigates the nutrient limitation of the microbial community, increasing soil microbial activity (Kamble et al. 2014; Li et al. 2016; Xie et al. 2017). Xie et al. (2017) concluded that maize straw application was successful in alleviating topsoil salinity. As straw decomposes, organic carbon fractions are released into the soil, promoting soil aggregation, increasing soil porosity, and reducing salt accumulation in the surface soil (Zhao et al. 2016a, Xie et al. 2017). Moreover, incorporation of a straw layer into the soil interrupts the continuity of capillary movement of salt from deeper soil layers and ultimately reduces salt levels in topsoil (Zhao et al. 2016b; Xie et al. 2017). Practices such as burying a straw layer also have a significant effect on soil water distribution. Zhao et al. (2016a) observed that use of a buried maize straw layer at a depth of 40 cm, combined with a plastic mulch cover, led to greater soil water content and significantly reduced salt content in the upper 40 cm depth, throughout the growth season of sunflower. Buried straw layer treatment alone induced a decrease in salt content in the early growth period (Zhao et al. 2016a). A buried straw layer combined with plastic mulching also had a positive effect on the microbial community, leading to significantly greater populations of bacteria, actinomyces, and fungi (Li et al. 2016). Recent findings have demonstrated that adoption of conservation agriculture practices—involving reduced tillage, residue retention, and crop rotation—have great potential to positively affect salt accumulation by reducing evaporation and upward salt transport (Devkota et al. 2015; Murphy et al. 2016). As soil water evaporates, it leads to salt accumulation on the surface. This process can explain the more pronounced soil salinization occurring

near the soil surface (10 cm) than in the top 90 cm soil fraction (Devkota et al. 2015). Therefore, the effect of crop residues on salt accumulation is more efficient up to 30 cm from the soil surface; below this depth, its effect is insignificant (Devkota et al. 2015).

Soil remediation can also be achieved through the addition of antisalinity agents such as Dinamic, Uni-sal, or humic acid applied through drip irrigation. Shahein et al. (2015) demonstrated that a combination of Dinamic and Uni-sal led to successful increases in the leaf nutrient profile, yield, fruit quality, shoot weight, and plant length in tomato plants irrigated with saline water (Shahein et al. 2015). In a similar study, the results obtained by El-Khawaga (2013) corroborated the positive influence of Uni-sal and other antisalinity agents such as Cal-Mor and citric acid on palm trees under salinity stress. Soil supplementation with sulfur also had a positive effect on date palm offshoots' tolerance of salinity, increasing accumulation of compatible solutes and chlorophyll content, which resulted in enhanced dry weight accumulation and water status (Abbas et al. 2015). The benefits of sulfur and sulfur-containing compounds could be related to their involvement in improving nutrient assimilation and stimulating ROS-scavenging activity through the sulfur metabolite glutathione (Khan et al. 2014; Abbas et al. 2015).

## 12.6 Conclusions

The development of new strategies to alleviate salinity in plants and stimulate crop cultivation under salinity stress is a relevant research purpose to face the needs of a world with growing soil salinity issues. Chemical, biological, and physical treatments are now available to address this challenge, being able to induce salinity tolerance at a systemic level, even if they are only applied on the seeds, roots, or leaves. Importantly, new agricultural practices focused on field and water management are also available to mitigate the harmful effects of excessive saline soils on growth and productivity of crops.

As described in this chapter, salinity can affect plant metabolic processes in different ways, depending not only on the time frame of the response to the salt constraint but also on the organ/tissue in which the response took place, as well as the plant genotype or species studied. A considerable number of studies have been aimed at understanding the molecular mechanism behind salinity tolerance in plants, with the ultimate goal being to reduce the effects of salinity on growth and yield (Munns and Tester 2008; Roy et al. 2014, Negrão et al. 2017). Physiological responses and biochemical networks involved in salt-tolerant plant responses to salinity have been revealed, and new salt stress-related genes have been made available for plant improvement.

The majority of the strategies described herein are seed treatments—also known as priming treatments—which trigger a physiological state that enables the growing plant to respond faster and in a more robust way when exposed to environmental constraints (Aranega-Bou et al. 2014; Savvides et al. 2016). Consequently, the

previous fundamental knowledge about how a plant reacts to the effects of a high salt concentration has been essential for the development of strategies for salinity alleviation. As we have described, treatments applied to alleviate the effects of salinity, aimed at accumulation of compatible solutes (e.g., proline and glycine betaine) or photosynthetic pigments, ROS scavenging (e.g., polyamines and antioxidant enzymes), or stimulation of ROS-mediated signaling cascades (e.g., H<sub>2</sub>O<sub>2</sub> accumulation) have been designed. Those approaches have been revealed to enhance the plant's ability to ensure water and nutrient uptake, photosynthesis, biomass accumulation and, ultimately, yield. An important future application of these “biomarkers” is that they can be used to monitor the suitability of new formulations or to screen for plant accessions that are better adapted to coping with saline conditions.

Omics technologies - global molecular profiling - applied to target plant species and crops can provide new insights into the molecular mechanism underlying plant adaptation to salinity. Transcriptomics, proteomics, and metabolomics are extending our knowledge of the molecular mechanisms associated with plant response to salinity. In time, they will reveal new target regulatory points that might possibly be modulated by the application of treatments “by design,” addressing the particularities of the soil and the crop's requirements. These approaches also need to be combined with an investment in new and sustainable agricultural practices that can ensure food security for local populations under the threat of the growing salinity scenario.

**Acknowledgements** Financial support from Fundação para a Ciência e a Tecnologia (Lisbon, Portugal) is acknowledged through the research unit “GREEN-it: Bioresources for Sustainability” (UID/Multi/04551/2013), a SSA postdoctoral grant (SFRH/BPD/108032/2015), a DM Plants for Life PhD grant (PD/BD/128498/2017), and a SFC research fellowship in the scope of the FCT project (PTDC/AGR-PRO/4261/2014).

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